



# JOURNAL OF AGRICULTURAL RESEARCH

## DEPARTMENT OF AGRICULTURE

VOL. V

WASHINGTON, D. C., NOVEMBER 1, 1915

NO. 5

### SOME POTATO TUBER-ROTS CAUSED BY SPECIES OF FUSARIUM

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#### INTRODUCTION

Deterioration of tubers of the Irish potato (*Solanum tuberosum*) is induced by a variety of causes. Economically the most important of these are the organisms *Phytophthora infestans*, *Fusarium* spp., bacteria, and miscellaneous fungi, including *Rhizopus nigricans*.

*Phytophthora infestans*, which is somewhat restricted to the northeastern part of the country, does more or less damage each year, and occasionally in epidemic form causes tremendous losses. Exclusive of *P. infestans*, however, species of *Fusarium* are undoubtedly the most important causes of tuber decay. Though never occurring in epidemic form with losses comparable to those of late-blight, they are present wherever potatoes are grown, taking their quota of the crop both in the field and in storage.

Several species of the genus *Fusarium* Link have been described as causes of tuber-rots of *Solanum tuberosum* (Clinton, 3; Pizzigoni, 12; Wehmer, 15; Smith and Swingle, 14; Pethybridge and Bowers, 11; Longman, 6; Manns, 7).<sup>2</sup> In most cases prior to 1912 *F. solani* (Mart.) Sacc. or some species thought to be a synonym of it is given as the causal organism. Until recently the chaotic condition of the genus *Fusarium* has precluded careful work with clearly defined species.

<sup>1</sup> Having been associated with Dr. H. W. Wollenweber, of the Bureau of Plant Industry, during the past two years, the writer has enjoyed the privilege of personal work with the species and strains cultivated during this period in connection with his monographic study of the genus *Fusarium*. Any attempt to work with the species of this form genus emphasizes the necessity of completing such studies. Owing to Dr. Wollenweber's absence during the preparation and publication of this paper, he is not responsible for the subject matter. It is regretted that his criticism of the results is lacking, particularly as the data obtained force the author to conclusions which differ somewhat from Dr. Wollenweber's published opinions.

<sup>2</sup> Reference is made by number to "Literature cited," pp. 208-209.

For a list of the more important references to potato studies, see the following: Appel, Otto. *Beiträge zur Kenntnis der Kartoffelpflanze und ihre Krankheiten*. I. 178 Arb. K. Biol. Anst. Land u. Forstw., Bd. 5, Heft 7, D. 419-435. 1907.

Conclusive work on species of *Fusarium* which produce tuber-rot with sufficiently delimited species dates from Appel and Wollenweber's fundamental work on the form genus *Fusarium*. During the progress of these studies Wollenweber established the wound parasitic nature of *Fusarium coeruleum* (Lib.) Sacc. and *F. discolor*, var. *sulphureum* (Schlecht.) App. and Wollenw., and the causal relation of these species to a definite type of rot. Jamieson and Wollenweber in 1912 (5) described an external dry-rot caused by *F. trichothecioides* Wollenw. Wollenweber in 1913 (19, 20) extended the list of species of *Fusarium* causing tuber-rot by the addition of the following: *F. ventricosum* App. and Wollenw., 1910, and *F. rubiginosum* App. and Wollenw., 1910 [considered a synonym of *F. culmorum* W. G. Sm., 1884, by Wollenweber, 1914 (21)]; *F. subulatum* App. and Wollenw., 1910, as a weak wound parasite under special conditions; *F. orthoceras* App. and Wollenw., 1910, and *F. gibbosum* App. and Wollenw., 1910, as probable causes of tuber-rot.

Jamieson and Wollenweber's description (5) of the powdery dry-rot caused by *F. trichothecioides* is the first description of a definite rot conclusively demonstrated to be caused by a species of *Fusarium* which is sufficiently described in its normal<sup>1</sup> stages to insure certain identification. However, Wilcox, Link, and Pool (17) published a description one year later of the same disease and subnormal stages of the same organism, for which they proposed a new name—i. e., *F. tuberivorum* Wilcox and Link. The examination of material similar to that used by Wilcox and Link from Alliance, Nebr., demonstrated that *F. tuberivorum* is identical with *F. trichothecioides*.

The increasing number of rotting tubers submitted to the Department indicated the existence of several types of a rot not hitherto described which were caused by species of *Fusarium* and focused the author's attention during the past year on a laboratory study of these diseases. The object of this paper is to demonstrate the parasitic nature of certain species of *Fusarium* and to contrast these organisms and the resulting types of deterioration with those already recognized. The economic importance of these rots and the interest manifested by pathologists in a general group of diseases caused by species of *Fusarium* suggested the advisability of a comprehensive treatment of the species known to cause decay as an aid to their diagnoses and ultimate control.

The tuber-rots considered in this investigation are all of the stem-end and wound-parasitic type. They are not sharply differentiated from each other nor from those previously described as caused by the following species: *F. coeruleum*; *F. discolor*, var. *sulphureum*; *F. trichothecioides*. After having made isolations from several hundred submitted specimens of stem-end-diseased tubers and from many more rotting as the result of wound and lenticel invasion or inoculation with known species, the

<sup>1</sup> For a discussion of the idea "normal" as used in this paper, see Wollenweber (21, p. 255-257).

author is convinced that in many cases the only sure way to determine the cause is by cultural studies. In general, specimens of the types of rot developed spontaneously in the field or storage are more characteristic than those produced by inoculation and developed under uniform conditions.

The powdery dry-rot with pink-mycelium-lined cavities caused by *F. trichothecioides* is quite characteristic and not easily confused with the others; the same is true of the rot produced by *F. discolor*, var. *sulphureum*, with its ochreous yellow mycelium, but the rot caused by *F. coeruleum*, in its typical form with external dark-blue mycelium masses and internal blue coloration of the tissues, may be easily confused with some of those herein described unless mature spores are found on the specimen or high cultures are obtained. On some tubers more than one of the wound-parasitic types of *Fusarium* are present; in others, the diagnosis is complicated by the secondary action of bacterial and fungous saprophytes. While the author can in typical cases determine the cause of *Fusarium* rot without the preparation of cultures, the latter is not infrequently the safer method. Our inability to differentiate surely the various rots macroscopically complicates the attempt to differentiate them as types caused by specific organisms.

#### METHOD OF TESTING PARASITISM

The method employed to demonstrate the wound-parasitic nature of species of *Fusarium* will be outlined in detail before proceeding with the discussion of the several types of tuber-rot and the inoculations with the causal organisms.

Sound tubers as free from skin diseases as possible were selected from the following varieties of potatoes: Burbank, Netted Gem, Early Rose, Idaho Rural, Jersey Peachblow, People's, and Pearl grown at Jerome, Idaho, in 1913 and 1914 and each year kept in cold storage at Washington, D. C., until needed; Irish Cobbler grown in Maine in 1913 and kept in storage through the winter; Green Mountain grown at Arlington, Va., in 1914 and used soon after harvesting.

The selected tubers were washed and disinfected in a solution of 0.5 per cent of formalin, in the majority of the experiments for half an hour, and rinsed in distilled water. Some tubers taken at random were wounded with a large platinum needle, dipped in distilled water, immediately wrapped in waxed paper, and placed in disinfected Altmann incubators. Other tubers were similarly wounded, dipped in distilled-water spore suspensions of the organism to be tested, wrapped, and placed with the controls.

By this method there are chances for secondary invaders, but the used organism is primarily the predominating one. In addition to the control tubers, in every case reisolation, identification in pure culture, and

reinoculation were depended upon to check the work. In many cases transfers of the original strains or of the reisolated ones, or of both, and of any intruders were made to raw, sterile cut potato blocks.

The identification of the closely related species of *Fusarium* employed in this work involved the careful preparation, purification, and morphological study of high cultures. The nutrient media found of most value in obtaining such cultures are as follows: Potato cylinders, rice, stems of cotton (*Gossypium* spp.), and sweet clover (*Melilotus alba*). Agar media were never used, except for plating. As emphasized by Dr. Wollenweber, the vegetable media are very valuable for encouraging characteristic development of species of *Fusarium*.

The control tubers were carefully examined for rot about the wounds. These tubers usually remained as sound as when placed in the incubator, only 4 out of some 140 used as controls having any rot whatever. Sprouting of the inoculated tubers and controls demonstrated their continued viability.

Throughout the incubation periods a maximum humidity was maintained, and necessarily the ventilation was bad. Readings of the temperatures were taken twice daily, and this factor is indicated by the average of all readings obtained from the particular compartment during the stated period. The temperatures were not constant, varying a degree or two above and below the average, but the average as recorded represents very nearly the actual storage temperature, since such fluctuations as occurred were of a temporary nature.

It may be considered by some pathologists that the method is an extreme one; that under the given conditions any organism might be expected to cause a rot. It is believed, however, that the conditions maintained are no more extreme than those to which potato tubers are frequently subjected in field and storage. The following facts tend to establish the validity of the method: (1) Certain organisms—for example, *F. moniliforme* Sheldon, *F. martii* (*sensu strict.*), *Verticillium albo-atrum* Reinke and Berthold, and *Sporotrichum flavissimum* Link—did not cause a rot under these conditions (see p. 201). (2) *F. solani*, *F. vasinfectum*, a species of *Mucor*, and one of *Rhizoctonia* were doubtfully wound-parasitic (see p. 192). (3) The wounded controls remained sound except in a few cases where they were in contact with badly rotted tubers; the same organism was isolated from such controls as from the inoculated tubers in the same compartment. (4) The species of *Fusarium* herein reported as wound parasites grow and rot sterile cut potato blocks in pure culture; none of the intruding organisms (bacteria or fungi) were able to do this, except that in a few cases the submerged part of the block was attacked. These facts, in addition to the experiments, seem to warrant the conclusions reached.

Since the tubers inoculated with the several species of *Fusarium* were treated uniformly and the rots developed by the respective species were

much alike, detailed accounts of the appearances presented are of doubtful value and are eliminated. With every rot-producing species of *Fusarium* included in the experiments the effect was essentially the same—at minimum temperatures, a slow dry-rot; at maximum, a very wet rot, with the tubers completely softened in two or three weeks. Sometimes in the former a mycelium-lined cavity is developed, surrounded by a zone of tissue appearing water-soaked—i. e., a zone of enzymic activity; in other tubers at higher temperatures the same organism proceeds to soften the tuber in a stratiform manner, the several layers reaching across the tuber. Bad-smelling rots did not occur with the species of *Fusarium*. Such rots associated with *Fusarium* spp. were found to be mixed infections. When *Fusarium* spp. *per se* rot potatoes, an odor suggesting ammonia and trimethylamin is developed.

Rots caused by species of *Fusarium* are commonly spoken of as either "dry-rots" or "wet-rots." The former are a result of comparatively slow development at low temperatures. The experiments show that any of these organisms capable of causing a rot work more rapidly in an environment of optimum temperature accompanied by high humidity, the tubers developing a wet-rot (see p. 196). Upon drying out, the condition would be termed a "dry-rot." The two forms grade insensibly into each other, so that neither term is specific. The examination of potato tissues rapidly softening as a result of inoculation with pure cultures of *Fusarium* spp. indicates that the middle lamella is dissolved considerably in advance of the fungus; the hyphæ ramify between the cells, but do not appear to enter them at once. Ultimately the contents of the cells are liberated, and the starch grains become more or less corroded.

It should be noted that the experimental data, revised and grouped under the respective organisms, were obtained through a series of experiments covering a period of more than a year. For example, the data on *F. oxysporum* (see p. 191) were extracted from eight different experiments which included several other species and show at a glance the comparative effect of original and reisolated strains on different varieties of potatoes at sundry temperatures.

In the notes on the artificial inoculations recorded under the respective organisms the history of the various strains is first outlined, followed by a brief consideration of the results in text and tabular form.

#### CERTAIN FIELD AND STORAGE ROTS OF POTATO TUBERS AND THEIR CAUSE

##### TUBER-ROT CAUSED BY *FUSARIUM* OXYSPORUM AND *FUSARIUM* HYPER- OXYSPORUM

In a study of a wilt and dry-rot of *Solanum tuberosum*, Smith and Swingle (14) attributed both manifestations to a species of *Fusarium*. After a consideration of the incomplete nature of previous descriptions

of species of *Fusarium* occurring on the potato, they chose the name of the earliest one for their fungus—i. e., *F. oxysporum* Schlechtendahl, 1824. This species was not differentiated from *F. solani* (Mart.) Sacc. and other species occurring on potatoes; although no inoculations are recorded by Smith and Swingle, *F. oxysporum* has been generally accepted as the cause of both the wilt and the dry-rot.

Manns (7) made inoculations with a species of *Fusarium* isolated from the blackened vascular ring and one from dry-rotting tubers, confirming the work of Smith and Swingle (14). He writes as follows (7, p. 316): "In the infection work both of the organisms were wilt producing, bringing about symptoms quite typical with that of the *Fusarium* blight in the field." Tuber-rot as a result of inoculation with a pure culture of his *Fusarium* sp. is not recorded. Like Smith and Swingle (14), he did not consider *F. oxysporum* different from *F. solani*.

Wollenweber (19, 20), after a study of *F. oxysporum* obtained from the vascular system of vines and tubers, was convinced that this species causes the wilt and stem-end ring discoloration, but not a tuber-rot. It simply winters over in the stem end of the tubers. A few quotations show his view regarding this species of *Fusarium*:

\* \* \* the fungus [*F. oxysporum*], a typical xylem inhabitant does not entirely destroy the tuber without the help of tuber rot Fusaria or bacteria [20, p. 42].

The fact that *F. oxysporum* causes the wilt of growing potato plants and only uses the xylem of the stem end of tubers for overwintering, without producing a rot of the parenchyma, leads to interesting comparisons \* \* \* [20, p. 42].

Referring to this fungus in his diagnosis, he states that it is a "\* \* \* vascular parasite, cause of wilt disease, but not tuber rot, of *Solanum tuberosum*" (20, p. 28).

To facilitate the arrangement of the species, Wollenweber (19, p. 32) established six provisional sections of the genus *Fusarium* based upon physiological and morphological characters. One of these sections, *Elegans*, comprises the vascular parasites, including *F. oxysporum*.

In general, Wollenweber's views in regard to *F. oxysporum* as indicated above are supported by the writer, but the experience of the last year indicates that these statements should be somewhat modified. The repeated isolation of *F. oxysporum* and related forms of the section *Elegans* from tubers rotting in field and storage, accompanied by the failure in many such cases to obtain any other organisms capable of producing a rot, indicates something more in the nature of this organism than passive hibernation in the vascular ducts of the stem end of potatoes. That the latter may be the chief rôle of the strain of *F. oxysporum* which causes wilt is not doubted. But there are strains of *F. oxysporum* and related forms present in stem-end ring disease and dry-rot which entirely destroy<sup>1</sup> the tubers under the experimental conditions outlined

<sup>1</sup> The fact that *F. oxysporum* is capable of destroying potato tubers is confirmed by Dr. Lou A. Hawkins, of the Bureau of Plant Industry, in unpublished studies on the chemistry of rots of *Fusarium* spp. He employed *F. oxysporum* 3395, a re-isolation of strain 2413 (see p. 190).

in another part of this paper. This statement is based upon the results of inoculation work with several strains of *F. oxysporum* isolated from various sources and includes two identified by Wollenweber—i. e., Nos. 1948 and 2413. (See p. 190 and Pl. XV, fig. 3.) The following species and varieties of the section *Elegans* were found to produce tuber-rot in varying degrees: (1) *F. oxysporum*. (2) A related form which differs by producing an abundant pionnotes on potato cylinders. (See p. 206 and Pl. XV, fig. 1, 2.) Morphologically this fungus is identical with *F. hyperoxysporum* (21, p. 268), described as a cause of stem-rot of the sweet potato (*Ipomoea batatas*) by Harter and Field (4, p. 287, 291). The experiments thus far carried out indicate its biological identity—i. e., *F. hyperoxysporum* isolated from *Ipomoea batatas* caused a similar rot under the same conditions. (See p. 192.) (3) *F. vasinfectum* Atkinson, the cause of cotton wilt. (4) Its homologue isolated from wilt of okra (*Abelmoschus esculentus*). The numerous forms of the section *Elegans* type, many of which appear to be morphologically identical but biologically different, require further study, and it is not proposed to enter into a taxonomic consideration of these forms at this time. (See p. 206.)

It seems probable that *F. oxysporum* is incapable of readily penetrating the wall of the xylem. When it enters the vascular ring of the tuber from the wilting mother plant, it hibernates therein during the resting period of the tuber and enters the sprouts with the renewal of vegetative activity. At other times as a wound or lenticel invader, plenty of suitable nourishment is at hand, and it produces a dry-rot or a wet-rot, according to the conditions of temperature and humidity. Possibly as a wound parasite it is without incentive or opportunity to enter the vascular ducts.

Although Smith and Swingle (14) and Manns (7) did not differentiate their *F. oxysporum* form *F. solani* and other species occurring on potato tubers, no evidence has been deduced to show that they were not in the main dealing with the effects of a single species or to prove that *F. oxysporum* does not cause a tuber-rot.

Further notes on *F. oxysporum* as a cause of tuber-rot are given under "Jelly-end rot" and in the experiments.

#### INOCULATION OF POTATO TUBERS WITH *FUSARIUM OXYSPORUM*, *FUSARIUM HYPEROXYSPORUM*, AND *FUSARIUM VASINFECTUM*

*FUSARIUM OXYSPORUM* Schlecht.—*F. oxysporum* 2997; isolated on March 10, 1914, from a tuber affected with stem-end ring disease and vascular necrosis, from Everest, Kan. Culture used, 16-day-old pionnotes on stem of *Melilotus alba*. As indicated in Table I, all tubers of the four varieties Jersey Peachblow, Idaho Rural, Early Rose, and People's were rotting after 19 days' incubation at an average temperature of 23.1° C. (See Pl. XV, fig. 3.) The least affected variety



was Idaho Rural. However, many of these were almost completely destroyed, being very mushy and "leaky."<sup>1</sup> The organism was recovered from all varieties, two reisolutions being made from the Rurals.

*F. oxysporum* 2999; isolated on March 14, 1914, from a tuber with wound-invading brownish dry-rot from Brookings, S. Dak. Culture, 16-day-old pionnotes on stem of *Melilotus alba*. The results were the same as with strain 2997. The organism was recovered in all attempts, reisolutions being made from all varieties except Early Rose.

*F. oxysporum* 3045; a reisolution of strain 2997 from a rotted tuber of the Idaho Rural variety 20 days after inoculation at 23.1° C. After incubating for 21 days at an average temperature of 25.6° C. all tubers of all varieties—i. e., Nettle Gem, Idaho Rural, and People's—showed a deep, progressive rot, a brown zone about the inoculation prick surrounded by a water-soaked area more or less brown in color. The organism was recovered by three isolations.

In a subsequent trial with strain 3045, inoculating the four varieties Idaho Rural, Nettle Gem, Burbank, and Pearl with a 1-month-old culture on a stem of *Melilotus alba* and incubating for 37 days at an average temperature of 20.4°, similar results were obtained. Seven reisolutions were identified from this lot.

*F. oxysporum* 1948; isolated and identified by Dr. Wollenweber from a secondary rot following infection by *Phytophthora infestans*. Material from Honeoye Falls, N. Y., February, 1913. Culture used was 1 month old on stem of *Melilotus alba*. The results at different incubation periods and temperatures are as follows: Ten tubers incubated for 24 days at an average temperature of 24.6° rotted, four slightly decaying in all punctures and six wet-rotting. Organism recovered. One tuber at 18.4° rotted in 51 days, while one at 17.8° failed to decay in this time, but the organism persisted.

*F. oxysporum* 2413; isolated and identified by Wollenweber in January, 1913, from a potato of the Up-to-Date variety, grown on Potomac Flats, Washington, D. C., in 1912, affected with the ring disease. Cultures used, one on stem of *Melilotus alba* and one on a potato cylinder 25 days old. Result of incubation at 25.7° C. for 14 days: All inoculated tubers decayed, 50 per cent being very badly decomposed with wet-rot; organism recovered by four reisolutions. Two tubers incubated at 17.8° and 18.4°, respectively, for 51 days suffered a rather dry rot; organism recovered.

*F. oxysporum* 3395; reisolution of strain 2413 from badly rotted Green Mountain potato tuber. Culture used, 4-day-old potato cylinders. Owing to the fact that certain of the tubers were rotting badly, the experiment was concluded before some of the others had started to decay. All of the Pearls, 95 per cent of the Nettle Gems, and 50 per cent of the

<sup>1</sup> Orton (9, p. 11) described a soft-rot caused by *Rhizopus nigricans*. Potatoes affected with this disease are called "leaky" or "melters."

Burbanks were rotting after incubation for 25 days at 23.5° C. Four reisolutions were made.

In Table I are given the results of inoculations with *F. oxysporum*.

TABLE I.—Results of the inoculation of different varieties of potatoes with original and reisolated strains of *Fusarium oxysporum*

Strain No.	Variety of potato.	Number of tubers.	Incubation period.	Average temperature.	Percentage of tubers rotting.
			Days.	°C.	
2997	Jersey Peachblow	4	19	23.1	100
	Idaho Rural	18	19	23.1	100
	Early Rose	5	19	23.1	100
	People's	5	19	23.1	100
2999	Jersey Peachblow	4	19	23.1	100
	Idaho Rural	17	19	23.1	100
	Early Rose	6	19	23.1	100
	People's	6	19	23.1	100
3045>2997	Netted Gem	9	21	25.6	100
	Idaho Rural	21	21	25.6	100
	People's	7	21	25.6	100
	Idaho Rural	4	37	20.4	100
3045>2997	Netted Gem	4	37	20.4	100
	Burbank	4	37	20.4	100
	Pearl	4	37	20.4	100
	Green Mountain	1	51	17.8	0
1948	do	1	51	18.4	100
	do	10	24	24.6	100
	do	1	51	17.8	100
	do	1	51	18.4	100
2413	do	10	14	25.7	100
	Burbank	10	25	23.5	50
	Netted Gem	19	25	23.5	95
	Pearl	17	25	23.5	100

>=reisolation of.

*FUSARIUM* Wollenw.—*F. hyperoxysporum* 3273; isolated in October, 1914, from a soft-rotting Irish potato from Ocean Springs, Miss. (Pl. XV, figs. 1, 2.) Cultures used for inoculation, pionnotes on 56-day-old culture on stem of *Melilotus alba* and a 10-day-old potato cylinder. After 14 days' incubation at an average temperature of 25.7° C. all tubers inoculated with this species were more or less wet-rotted about the inoculation pricks and the lenticels, two tubers being completely softened. The organism was recovered by four reisolutions. Fifty-one days' incubation at temperatures ranging from 16.3° to 18.4° gave a slight rot in all. A gradual increase was observed with the increase in temperature. At 18.4° all were rotted, one being completely destroyed. Four reisolutions were made.

*F. hyperoxysporum* 3343; reisolation of strain 3273, from rotting Green Mountain potato tubers 15 days after inoculation at 25.7°. Culture used, a 26-day-old stem of *Melilotus alba* with pionnotes. All of the inoculated tubers of the four varieties Idaho Rural, Netted Gem, Burbank, and Pearl were rotted after an incubation period of 28 and 37

days at average temperatures of 19.7° and 20.4°, respectively. Seven reisolations were identified.

*F. hyperoxysporum* 3399; isolated from *Ipomoea batatas* from Lincoln, Ark., by Mr. L. L. Harter. Determined by Miss Ethel C. Field and the author. Culture used for inoculation, 20-day-old cotton stem. As given in Table II, after 51 days' incubation at an average temperature of 21.5°, the results were as follows: Of the four inoculated tubers of each of the varieties Idaho Rural, Netted Gem, Burbank, and Pearl 0, 1, 1, and 4 tubers were rotting, respectively. The organism was recovered by four isolations.

*F. hyperoxysporum* 3489; reisolation of strain 3399. Culture used for inoculation, 8-day-old potato cylinder and rice culture. This strain was considerably more active than the parent strain 3399. All tubers were rotted after an incubation of 25 days at 23.5°. Six reisolations were made.

Table II gives the results of the inoculations with *F. hyperoxysporum*.

TABLE II.—Results of the inoculation of different varieties of potatoes with original and reisolated strains of *Fusarium hyperoxysporum*

Strain No.	Variety of potato.	Number of tubers.	Incubation period.	Average temperature.	Percentage of tubers rotting.
			Days.	°C.	
3273.....	Green Mountain.....	4	51	16.3	100
		4	51	17.0	100
		4	51	17.8	100
		4	51	18.4	100
		10	14	25.7	100
3343>3273.....	Idaho Rural.....	4	28	19.7	100
		4	28	19.7	100
		4	27	20.4	100
		4	37	20.4	100
		4	51	21.5	0
3399.....	Netted Gem.....	4	51	21.5	25
		4	51	21.5	25
		4	51	21.5	100
		4	51	21.5	100
		9	25	23.5	100
3489>3399.....	Pearl.....	25	25	23.5	100
		22	25	23.5	100

>=reisolation of.

*FUSARIUM VASINFECTUM* Atk.—Inoculations were made with *F. vasinfectum* isolated from cotton and a similar organism from okra to determine whether this species, which is closely related to *F. hyperoxysporum*, would cause a decay of potatoes. Although considerable decomposition occurred in the inoculated tubers, a scrutiny of the data summarized below reveals the nonconclusive nature of the results obtained.

*F. vasinfectum* 1855; reisolated by Dr. Wollenweber, in December, 1912, from the vascular system of a cotton plant wilting as a result of

inoculation with strain 1733, a reisolation of strain 1635, which in turn was a reisolation of an original strain 1485 obtained from the discolored vascular system of the main root of a wilting cotton plant from Florence, S. C., on June 15, 1912. Culture used, 26-day-old pionnotes on stem of *Melilotus alba*.

*F. vasinfectum* 3167; reisolation of 1855, on June 19, 1914, from Idaho Rural potato in above experiment, after 25 days' incubation at 25.5° C. Culture used, 19-day-old pionnotes on a potato cylinder.

The results with tubers inoculated with *F. vasinfectum* 1855 after an incubation period of 25 days at an average temperature of 25.5° were as follows: The five tubers of the Netted Gem variety remained sound; one of the three tubers of the Idaho Rural variety and all of the People's variety were rotted, the organism being recovered from both varieties. With strain 3167, one of these reisolations, only 75 per cent of the tubers of the Pearl variety were rotted after 51 days' incubation at an average temperature of 21.5° C. These tubers were attacked only where a comparatively large cut surface had been exposed to the inoculum. The organism was recovered in each attempt, three reisolations being made.

*F. vasinfectum* 3263; isolated in September, 1914, as a particularly virulent strain of the cotton-wilt fungus from supposedly wilt-resistant cotton obtained in breeding experiments from Denmark, S. C. Culture used, 20-day-old potato cylinder.

*F. vasinfectum* 3243; isolated on September 5, 1914, from the vascular bundles of a wilting okra plant from Wrightsboro, N. C. Culture used, 20-day-old potato cylinder.

With *F. vasinfectum*, strains 3263 and 3243, the results were less conclusive. In tubers inoculated with the former strain the organism persisted for 41 days at average temperatures of 18.3° and 18.9° without perceptible damage. Of 10 tubers at 23.5° for 41 days, 5 were rotted, the organism being recovered from 3 of them and *F. radicola* being isolated from 2. The organism persisted in the other 5 tubers, though no rot resulted. With strain 3243 the organism persisted for 51 days at 17.8° and 18.4° without damage to the tubers. One tuber at 24.6° for 24 days was badly rotted, and the organism was recovered; of 9 tubers at 23.5° for 41 days, only one rotted. The organism was not recovered, but *F. radicola* was isolated.

In this connection it may be noted that in one experiment (p. 202), which included *F. vasinfectum* 1855 and two strains of *Verticillium albo-atrum* among other organisms, some of the tubers inoculated with the species of *Verticillium* and likewise certain controls rotted; from these the organism used could not be recovered, but *F. vasinfectum* was isolated several times.

Table III gives the data of the inoculations with *F. vasinfectum*.

TABLE III.—Results of the inoculations of different varieties of potatoes with original and reisolated strains of *Fusarium vasinfectum*

Strain No.	Variety of potato.	Number of tubers.	Incubation period.		Average temperature.	Percentage of tubers rotting.
			Days.	°C.		
1855.....	Netted Gem.....	5	25	25.5	0	
	Idaho Rural.....	3	25	25.5	33	
	People's.....	5	25	25.5	100	
	Idaho Rural.....	4	51	21.5	0	
3167>1855.....	Netted Gem.....	4	51	21.5	0	
	Burbank.....	4	51	21.5	0	
	Pearl.....	4	51	21.5	0	
	Green Mountain.....	1	41	18.3	75	
3263.....	.....do.....	1	41	18.0	0	
	.....do.....	10	41	23.5	0	
	.....do.....	1	51	17.8	50	
	.....do.....	1	51	18.4	0	
3243.....	.....do.....	9	41	23.5	10	
	.....do.....	1	24	24.6	100	

&gt;—reisolation of.

JELLY-END ROT AND A TUBER DRY ROT CAUSED BY *FUSARIUM RADICICOLA*

## JELLY-END ROT

"Jelly-end" is the very appropriate name applied by growers to potatoes affected with a field rot and a storage rot which annually cause serious losses in the delta lands of California and in the irrigated sections of Oregon and Idaho.

Many of the tubers when dug show the characteristic soft rot at the stem end, the affected portion easily separating from the rest of the tuber (Pl. XVI, XVII). The rot proceeds uniformly until the whole tuber becomes a slimy mass within the entire skin. If allowed to dry out, the skin sometimes persists as a loose attachment at the stem end, or it may shrivel and wrinkle down on the affected part, in this stage suggesting dry rot.

The jelly-end rot is not a new disease, but nothing has been done to establish the cause of the trouble. Orton (9, p. 5), discussing the wilt and dry end-rot of potatoes in California, says: "An early form of this *Fusarium* dry end-rot is frequently met with shortly after digging, and potatoes thus affected are known to buyers as 'jelly-ends.'" Shear (13, p. 6) says: "A serious feature of this disease [wilt] is that it forms a means of entrance for other fungous and bacterial diseases of the tubers, such as 'jelly-end' and dry rot." The examination of specimens from different localities indicates that jelly-end rots may be caused by several species of *Fusarium*. Wollenweber (21, p. 257-258, 264-265) isolated both *F. orthoceras* and *F. radicicola*, and of this disease he says in part (p. 265):

In Watsonville, Cal., in October, 1913, the writer found up to 80 per cent of Burbank potatoes in a large acreage affected by this peculiar soft rot, which is quite different

from that produced by *F. coeruleum* and other species \* \* \*. In tubers with the jelly-end rot *F. orthoceras* is often, but not always, associated with such fungi as *F. radiculicola*, *Mycosphaerella solani*, *Sporotrichum flavissimum* Lk., *Rhizoctonia*, and also with bacteria.

Concerning *F. radiculicola*, he says (p. 258):

It is often isolated from Irish potato, especially from dry tubers affected with stem-end dry rot. Sometimes it is associated with other organisms, but frequently seems to invade the tuber from the stolon before a cork layer has been formed \* \* \*. Its presence in the sweet potato suggests that it might require a higher optimum temperature than its related species, such as *F. solani* and *F. martii*.

*F. radiculicola*, *F. oxysporum*, *F. moniliforme* Sheldon, and *Rhizoctonia* sp., together with various saprophytic fungi and bacteria, were isolated by the writer from jelly-end rots from Watsonville and Moorland, Cal. *F. orthoceras*, *Mycosphaerella solani*, and *Sporotrichum flavissimum* were not obtained from such tubers.

*F. radiculicola* was most frequently obtained from typical "jelly-end" tubers from California and Idaho. Its ubiquitous nature and its behavior in all of the inoculation experiments support the view that it is one of the most important causes of this disease. The relation of this species to other tuber rots is discussed in the paragraph on dry-rot.

The prevalence in California of wilt caused by species of *Fusarium* and the frequency with which *F. oxysporum* was isolated from jelly-end rot suggests the fundamental relationship of this species to the disease. *F. oxysporum* was isolated and identified 24 times from jelly-end rot and stem-end dry-rot tubers from California alone. While often associated with bacteria and fungus saprophytes, in most of these cases it was the only organism secured from the respective tubers which could be regarded as the cause of the condition. It was frequently present in pure culture at the border of rotting and healthy tissues. Whether unaided it produces jelly-end rot under field conditions is not known. A potato tuber from California was diagnosed as ring disease and placed in the incubator. After a period of two months at an average temperature of 18.36° C. a typical jelly-end rot had developed. *F. oxysporum* was the only organism secured from the interior of this tuber at the border of healthy tissue. The inoculation experiments with *F. oxysporum* support the view that it is capable of producing jelly-end rot. *F. radiculicola* and *F. oxysporum* were also isolated, though not necessarily in association, from rot areas on the side of tubers resulting from wounds and lenticel invasion.

#### DRY-ROT

*F. radiculicola* as a cause of stem-end dry-rot was first obtained in August, 1913, from some tubers submitted from Grassfield, Va. Its widespread occurrence in stem-end dry-rotting tubers may be judged from the following distribution: Hermiston, Oreg.; Watsonville and Sonora, Cal.; Fallon, Nev.; Ocean Springs, Miss.; Jerome, Idaho; Honeove

Falls, N. Y.; Potomac Flats, Washington, D. C.; Arlington, Va.; etc. It enters the stem end of the tubers most commonly, but also invades lenticels and wounds. In some cases the affected tissue is light colored and soft, suggesting bacterial rot—i. e., practically the jelly-end rot. More often in the East it is characterized externally by a firm sunken area with the underlying parenchyma brown to black, dry, tough, and sharply differentiated from the healthy tissue.

This stem-end wound and lenticel dry-rot caused by *F. radicicola* may be regarded as a form of jelly-end rot. The organism is one of the causes of jelly-end rot, but the field and storage conditions where it occurs are different. Under conditions of high humidity the rot is of the jelly-end type; where the humidity or temperature is low and the action of the fungus less rapid, dry-rot develops, the affected tissue being more firm and darker colored as a result of drying and oxidation. (See p. 197, Pl. XV, fig. 4, 5.) Both types occur in California, Oregon, and Idaho, sections under irrigation. The dry-rot phase was the one most frequently submitted for diagnosis from other localities—i. e., of presumably slower development at lower temperatures.

#### INOCULATION OF POTATO TUBERS WITH *FUSARIUM RADICOLA*

*F. radicicola* 2842; isolated in October, 1913, from jelly-end rot of Burbank potato from Middle River, Cal. Unfortunately, the number of tubers in the experiment with this strain was not recorded. About 1 peck of potatoes of the Burbank variety and  $\frac{1}{2}$  peck of the Netted Gem variety were used for inoculation and controls. The tubers were incubated at temperatures ranging from 14° to 20.3°; average lowest compartment, 16.7°; highest, 18.2° C. After 37 days' incubation only one tuber showed a rot; this was at an average temperature of 18.2° C. The organism was recovered.

The thirty-eighth day after inoculation the remaining tubers were exposed to an average temperature of 22.8° C. for the succeeding 19 days. At this time all inoculated tubers were rotted, all stages of wet-rot and dry-rot being represented. The Netted Gems were more badly affected than the Burbanks. In every case the organism was recovered where the attempt was made, four reisolutions being identified.

*F. radicicola* 2890; isolated in October, 1913, from a jelly-end rotted tuber of the Burbank variety from Watsonville, Cal. (associated with *Rhizoctonia* sp. 2892). Culture used, 9-day-old pionnotes on a stem of *Melilotus alba*. All inoculated tubers showed a progressive rot beginning at the inoculation prick (Pl. XVII) after 20 days' incubation at an average temperature of 23° C. The lenticels were invaded and the sprouts infected and dropping off. Some of the tubers were completely softened, only a slimy mass remaining in the entire skin. The organism was recovered by six reisolutions.

*F. radicicola* 2890 plus *Rhizoctonia* sp. 2892. The two organisms were used in combination, 14 tubers being inoculated and incubated as above. More advanced decomposition seemed to take place than when *F. radicicola* alone was present. However, the species of *Rhizoctonia* could not be recovered, but *F. radicicola* was reisolated wherever the attempt was made.

*F. radicicola* 3021; reisolation of 2890 from a Burbank potato 20 days after inoculation with the latter. With this reisolated strain an attempt was made to ascertain the effect of the temperature factor on the action of the organism. The inoculated tubers (Irish Cobbler variety) were badly decomposed at average temperatures of 23.3°, 20.2°, and 19.5° C. At 18.7° the majority were more seriously affected than at lower temperatures; indeed, at 17.5° and 15.1° the effect was a slow dry-rot, while at 12.5° the organism persisted for 88 days without perceptible damage to the host.

*F. radicicola* 3023. Another reisolation of strain 2890; from lenticel infection after 20 days' incubation at 23° C. All tubers of the three varieties Netted Gem, Idaho Rural, and People's inoculated with this strain and incubated for 21 days at an average temperature of 25.6° were very badly decomposed. The organism was recovered by three isolations.

*F. radicicola* 2998; isolated March, 1914, from a stem-end ring disease and wound-infected tuber from Fallon, Nev. Culture used, 12-day-old pionnotes on stem of *Melilotus alba*. All tubers inoculated with this strain and incubated 20 days at 23° C. rotted. The organism was recovered.

*F. radicicola* 3236; isolated in August, 1914, in association with *F. hyperoxysporum* from a soft-rotting tuber from Ocean Springs, Miss. Culture used, 1-month-old potato cylinder. The results with this strain are as follows: One tuber incubated for 14 days at 25.7° was badly softened with wet-rot. The organism was recovered. Nine tubers at 24.6° for 24 days were slightly rotted in every inoculation prick, one tuber being completely softened with grayish wet-rot. Organism recovered by two reisolations. Sixteen tubers incubated 51 days at temperatures ranging from 16.3 to 18.4° C. gave the following results: At lowest temperature no rot occurred, but the organism had become established; two of the four tubers at 17° were rotting slightly, with the organism established in the others; at 17.8°, two were slightly rotted, with the organism persisting in the others; at 18.4° one tuber was sound and the three others were rotting.

*F. radicicola* 2862; isolated October, 1913, from jelly-end rot of a tuber of the Burbank variety from Sargent Island near Middle River, Cal. Culture used, 9-day-old pionnotes on stem of *Melilotus alba*. This strain was comparatively inactive, only 12 per cent of the inoculated tubers rotting after 20 days' incubation at 23° C. The organism was recovered.



*F. radicola* 3319; isolated November, 1913, in association with *Mucor* sp. 3320 from a "leaky" diseased potato tuber from Moorland, Cal. Culture used, 1-month-old pionnotes on a potato cylinder. This strain was similar to 2862, being comparatively inactive. After 51 days' incubation at 21.5 C., only 1 tuber of 16 inoculated developed a rot. No attempt was made to recover the organism.

The results of the inoculations with *F. radicola* are given in Table IV.

TABLE IV.—Results of inoculation of different varieties of potato with original and reisolated strains of *Fusarium radicola*

Species and strain No.	Variety of potato.	Number of tubers.	Incubation period.	Average temperature.	Percentage of tubers rotting.
			Days.	°C.	
<i>Fusarium radicola</i> 2890.	Burbank.....	20	20	23.0	100
<i>Fusarium radicola</i> 2890 and <i>Rhizoctonia</i> sp. 2892.	.....do.....	14	20	23.0	100
<i>Fusarium radicola</i> 3301>2890.	Irish Cobbler.....	5	24	23.3	100
		10	88	20.2	100
		10	88	19.6	100
		25	88	18.7	100
		10	88	17.5	100
		6	88	15.1	100
		6	88	12.5	0
<i>Fusarium radicola</i> 3023>2890.	(Netted Gem.....	10	21	25.6	100
	Idaho Rural.....	14	21	25.6	100
	People's.....	4	21	25.6	100
<i>Fusarium radicola</i> 2998.	Burbank.....	8	20	23.0	100
<i>Fusarium radicola</i> 3236.	Green Mountain....	4	51	16.3	0
		4	51	17	50
		4	51	17.8	50
		4	51	18.4	75
		1	14	25.7	100
		9	24	24.6	100
<i>Fusarium radicola</i> 2862.	Burbank.....	25	20	23.0	12
	Idaho Rural.....	4	51	21.5	0
<i>Fusarium radicola</i> 3319.....	Netted Gem.....	4	51	21.5	25
	Burbank.....	4	51	21.5	0
	Pearl.....	4	51	21.5	0

>=reisolation of.

#### A NEW DRY-ROT CAUSED BY *FUSARIUM EUMARTII*

A type of field and storage rot hitherto undescribed was frequently observed in the examination of potatoes from Pennsylvania during the last two years. The character of this rot is as follows: In mild infection of the stem end the tuber shows externally a darkened sunken area with a greenish luster about the stolon insertion. If a thin slice is cut at this point, the parenchyma and the vascular ring are seen to be browned to varying depths. Some of the bundles are discolored to a greater depth

than the parenchyma and are darker in color, sometimes almost black. In this state the condition might be mistaken, and probably has been in the past, for stem-end ring disease caused by *F. oxysporum* or *Verticillium albo-atrum*, or for one phase of net necrosis (10, p. 14), which it more closely resembles. By the culture method, however, a species of *Fusarium* is invariably obtained from such tubers at the border of diseased and healthy tissues. The name "*Fusarium eumartii*" is proposed for this fungus.

In the more advanced stages of rot caused by *F. eumartii* the end of the tuber or the entire tuber is involved (Pl. XVIII). According to the humidity and other environmental conditions, the rot is (1) soft and light-brown or (2) dry, corky to friable, and dark-brown to almost black. In general, the rot proceeds uniformly as a sharply differentiated layer easily removable when moist, but close-clinging when dry. In field material the bundles are often discolored as above noted, in advance of the rot. Attempts to isolate the organism from the tips of such bundles usually failed. In the experiments the rot is preceded by a moist water-soaked zone of enzymic activity, from the border of which no organism was obtained. No difficulty was experienced in isolating *F. eumartii* from the border of the discolored tissue and the watery zone.

Considerable care is necessary to differentiate this rot from the one caused by the closely related *F. radicola*. Sometimes the determination is to be decided only by the careful preparation and study of high cultures. The morphological differences between *F. eumartii* and *F. radicola* are discussed on page 205.

*F. eumartii* is chiefly a stem-end and wound invader, but under favorable conditions the lenticels become infected. The fact that *F. oxysporum* was sometimes obtained in association with this fungus and the further fact that this disease of the tubers is reported on plants described as having symptoms of wilt suggest the probable relationship of *F. oxysporum* to the trouble. A field study of wilt and the relation of *F. oxysporum* to such field rots and storage rots should throw considerable light on the problem.

Attempts to isolate an organism from a type of stem-end necrosis similar to mild cases of invasion with *F. eumartii* often failed. There seems to be a sterile necrosis of the stem end, accompanied by browning of the parenchyma and bundles, which is related to the disease described as net necrosis (10, p. 14, pl. 2). Sometimes this type of stem-end necrosis can be distinguished from slight infection with *F. eumartii* only by the culture method; but when the minute ramifications of the vascular ducts are discolored, resulting in the characteristic phase of net necrosis, it can not be confused with the new type of rot.

This rot was obtained chiefly in Pennsylvania, the following localities representing its known distribution: Tower City and Orwigsburg, Schuylkill County, Pa.; East Greenville, Montgomery County, Euclid,

Butler County, and in Dutchess County, N. Y. To judge from correspondence with growers it is a field rot and a storage rot of considerable importance. Infected tubers placed in storage rot badly the following spring; some of the growers are reported to have lost 50 per cent from dry-rot. Whether unaided *F. eumartii* produces a wilt and a rot as a result of planting infected seed is not known. More likely it is secondary to infection by *F. oxysporum* or *Verticillium albo-atrum* in such cases.

#### INOCULATION OF POTATO TUBERS WITH *FUSARIUM EUMARTII*

*F. eumartii* 2932; isolated on January 3, 1914, from a stem-end dry-rotting tuber (Heath's Medium-Late Surprise variety) from Tower City, Pa. Culture used, 7-day old pionnotes on cotton stem.

*F. eumartii* 2947; isolated as above on January 15, 1914. Culture used, 7-day-old pionnotes on potato cylinder.

*F. eumartii* 3040; reisolation of 2947, April 23, 1914, from rotting Idaho Rural potato, 19 days after inoculation at 23.1° C. Cultures used, 22-day-old pionnotes on potato cylinder, and in a subsequent trial 2-months-old cultures on rice, *Melilotus alba*, and cotton stems.

*F. eumartii* 2958; isolated on January 28, 1914, as recorded in Nos. 2932 and 2947. Culture used, 7-day-old pionnotes on potato cylinder.

All tubers of the five varieties mentioned which were inoculated with the several original and reisolated strains of this species of *Fusarium* showed a progressive rot beginning at the points of inoculation in each case; many of the lenticels were invaded, sunken, and with the subjacent parenchyma browned. People's variety was the most susceptible, the others being affected in the order named—Early Rose, Jersey Peachblow, Netted Gem, and Idaho Rural (Pl. XIX). However, even in the last-mentioned variety there was 100 per cent of infection about the inoculation pricks and lenticel invasion of all tubers. Some of the inoculated tubers were completely softened; others showed a dark-brown zone about the inoculation prick, surrounded by an extensive watery zone of softened tissue. At low temperatures a typical slow dry-rot was produced. The respective organisms were recovered in every attempt made: Nos. 2932 and 2947 from all varieties used; 2958 from the Idaho Rurals; 3040 in first trial, one reisolation from the Idaho Rurals, and one from the Netted Gems; in a later experiment five reisolations were made from the Idaho Rural variety.

Table V gives the results of the inoculations with *F. eumartii*.

TABLE V.—Results of the inoculation of different varieties of potatoes with original and reisolated strains of *Fusarium eumartii*

Strain No.	Variety of potato.	Number of tubers.	Incubation period.	Average temperature.	Percentage of tubers rotting.
			Days.	°C.	
2932.....	Jersey Peachblow...	3	19	23.1	100
	Idaho Rural.....	14	19	23.1	100
	Early Rose.....	4	19	23.1	100
	People's.....	4	19	23.1	100
2947.....	Jersey Peachblow...	4	19	23.1	100
	Idaho Rural.....	19	19	23.1	100
	Early Rose.....	4	19	23.1	100
	People's.....	4	19	23.1	100
3040>2947.....	Netted Gem.....	4	19	23.1	100
	Idaho Rural.....	9	21	25.6	100
	People's.....	14	21	25.6	100
		5	21	25.6	100
3040.....	Idaho Rural.....	15	65	13.8	100
		15	65	17.2	100
		15	65	18.6	100
	Jersey Peachblow...	3	19	23.1	100
2958.....	Idaho Rural.....	18	19	23.1	100
	Early Rose.....	3	19	23.1	100
	People's.....	3	19	23.1	100
		3	19	23.1	100

>—reisolation of.

### CONTROL INOCULATIONS OF POTATO TUBERS

In order to ascertain whether any organism at random would cause a decay of potato tubers under the conditions used to establish the wound-parasitic property of the species mentioned, certain species of *Fusarium* and other organisms inhabiting potato tubers were included in the experiments. The following organisms were used for this purpose: *F. martii*, *F. solani*, *F. moniliforme*, *Verticillium albo-atrum*, *Sporotrichum flavissimum*, a species of *Mucor*, and a species of *Rhizoctonia*. The notes on the effect of these organisms on different varieties of potatoes at sundry temperatures are extracted from the several experiments and grouped according to organism as a support of the method. It may be mentioned in this connection that certain strains of *F. radicola* (Nos. 2862 and 3319) were found to be comparatively inactive under conditions identical with those in which other strains were most virulent.

### INOCULATION OF POTATO TUBERS WITH CERTAIN SPECIES OF *FUSARIUM* AND OTHER TUBER-INHABITING ORGANISMS

*F. solani* 176; isolated in 1908 by Dr. Wollenweber at Dahlem, near Berlin, Germany, from a potato tuber. Used for the original description of this species by Appel and Wollenweber (1, p. 77). Culture used, 2-months-old pionnotes on potato cylinder. After 51 days at an average temperature of 21.5° C., this organism had attacked only 50 per cent of but one variety, Pearl, and then only where a large cut surface was

exposed. In other words, but 2 tubers of 16 inoculated were rotted. From the two affected tubers *F. solani* was recovered once, *F. radicola* was isolated twice, and *F. oxysporum* once.

*F. martii* 186; isolated from *Pisum sativum* in April, 1910. Sent to Dahlem, Germany, by Miss J. Westerdijk, of Amsterdam, Netherlands, as *F. vasinfectum*, var. *pisi* Van Hall; determined by Dr. Wollenweber. Culture used, 2-months-old pionnotes on potato cylinder. None of the 16 tubers inoculated was affected after 51 days' incubation at an average temperature of 21.5° C.

*F. moniliforme* 3321; isolated on November 3, 1914, in association with *F. radicola* 3319 and *Mucor* sp. 3320 from a "leaky" (see footnote, p. 190) tuber from Moorland, Cal. Culture used, 1½-months-old cotton stem culture. Of the 16 tubers inoculated, none was rotted after 41 days at an average temperature of 21.5° C.

*Verticillium albo-atrum* 1717 and 2784. The former strain was isolated by Dr. Wollenweber in September, 1912, from the discolored vascular bundles of wilting okra plant from Monetta, S. C. Strain 2784 was isolated on August 28, 1913, from a wilting potato plant of the Rural variety from Greeley, Colo. After an incubation period of 25 days at an average temperature of 25.5° C. the tubers of the Netted Gem and Idaho Rural varieties inoculated with the respective strains remained sound. The tubers of the People's variety inoculated with these strains were badly rotted in both cases. The organisms could not be recovered, but *F. vasinfectum* was isolated. Tubers inoculated with the latter species were in the same compartment.

*Sporotrichum flavissimum* 1455; isolated and determined by Dr. Wollenweber in May, 1912; from a hollow Irish Cobbler potato from Arlington, Va. Culture used for inoculation, 2-weeks-old potato cylinder. Of 12 tubers inoculated with the organism and incubated for 20 days at 23° C., none was rotted.

*Mucor* sp. 3320; isolated on November 3, 1914; from same source and in association with *F. moniliforme* 3321 and *F. radicola* 3319. Culture used, 2-months-old fruiting culture on cotton stem. Two tubers out of 16 inoculated with this organism were rotted after incubating for 51 days at 21.5° C. From these the organism was recovered by one re-isolation, and *F. oxysporum* and *F. vasinfectum* were isolated each once. Tubers inoculated with the latter species were in the same compartment.

*Rhizoctonia* sp.; for inoculation results with this organism see p. 197.

In Table VI are given the results of the inoculations with the species of *Fusarium* and other potato-inhabiting organisms.

TABLE VI.—Results of the inoculation of different varieties of potato tubers with certain species of *Fusarium* and other tuber-inhabiting organisms

Species and strain No.	Variety of potato.	Number of tubers.	Incubation period.	Average temperature.	Percentage of tubers rotting.
			Days.	°C.	
<i>Fusarium solani</i> 176.	Idaho Rural.....	4	51	21.5	0
	Netted Gem.....	4	51	21.5	0
	Burbank.....	4	51	21.5	0
	Pearl.....	4	51	21.5	0
<i>Fusarium martii</i> 186.	Idaho Rural.....	4	51	21.5	a 50
	Netted Gem.....	4	51	21.5	0
	Burbank.....	4	51	21.5	0
	Pearl.....	4	51	21.5	0
<i>Fusarium moniliforme</i> 3321.	Idaho Rural.....	4	41	21.5	0
	Netted Gem.....	4	41	21.5	0
	Burbank.....	4	41	21.5	0
	Pearl.....	4	41	21.5	0
<i>Verticillium albo-atrum</i> 1717.	Netted Gem.....	4	41	21.5	0
	Idaho Rural.....	4	25	25.5	0
	People's.....	4	25	25.5	0
	.....	5	25	25.5	a 100
<i>Verticillium albo-atrum</i> 2784.	Netted Gem.....	4	25	25.5	0
	Idaho Rural.....	3	25	25.5	0
	People's.....	5	25	25.5	0
<i>Sporotrichum flavissimum</i> 1455.	Burbank.....	12	25	25.5	a 60
	.....	12	20	23.0	0
<i>Mucor</i> sp. 3320....	Idaho Rural.....	4	51	21.5	0
	Netted Gem.....	4	51	21.5	0
	Burbank.....	4	51	21.5	a 25
	Pearl.....	4	51	21.5	0

<sup>a</sup> The respective organism is doubtfully the cause, as in each case wound-parasitic species of *Fusarium* were isolated in association. See text.

#### TAXONOMIC ARRANGEMENT AND DIAGNOSTIC CHARACTERS OF IMPORTANT ROT-PRODUCING SPECIES OF *FUSARIUM*

##### *FUSARIUM* Link

The sections Martiella, Elegans, and Discolor provisionally established by Wollenweber (19, p. 32; 20, p. 28) include the species of *Fusarium* causing tuber-rot known to be economically important. Certain other species—namely, *F. ventricosum*, *F. gibbosum*, *F. culmorum*, *F. orthoceras*, and *F. subulatum*—reported by Wollenweber (19, 20) as weak wound parasites of the Irish potato are not included in the following arrangement of species. *F. solani*, the type species of the section Martiella, is listed because of its ubiquitous occurrence on potatoes as well as on roots and tubers of other plants. Subnormal conidia of *F. coeruleum*, *F. radicola*, and *F. eumartii* are easily confused with those of *F. solani*. The form, size, and septation of normal conidia must be depended upon for differentiation.

## A. SECTION MARTIELLA

[Species in this section are *F. solani* (Mart.) Sacc., *F. martii* App. and Wollenw., *F. eumartii*, n. sp., *F. coeruleum* (Lib.) Sacc., and *F. radicleola* Wollenw.]

1. *Fusarium solani* (Mart.) Sacc. (1, p. 77).

Conidia normally triseptate (Pl. XIV, fig. 3) up to 100 per cent, occurring in pionnotes and sporodochia,<sup>1</sup> averaging 30 to 40 by 5 to 6 $\mu$ . Limits of normal triseptate conidia: 25 to 45 by 4.5 to 6.5 $\mu$ . Seldom 2 and 4, exceptionally 1 and 5 septate (limits: 1-septate, 15 by 4 $\mu$  minimum; 5-septate, 59 by 6.5 $\mu$  maximum; greatest width, 7 $\mu$ ; highest septation, 7.) Conidial mass brownish white, becoming brown in age; often greenish as a result of infiltration with greenish blue pigment from the plectenchymatic mycelium. Chlamydospores terminal, intercalary, and conidial; unicellular, round or pear-shaped, 8.5 by 8 $\mu$ ; 2-celled with constriction at cross wall, 12 by 7.75 $\mu$ ; smooth, rarely in chains or clumps.

*Habitat*.—On decaying tubers and roots of plants and in the soil. Isolated from species of *Solanum*, *Citrullus*, *Cucumis*, *Cucurbita*, *Lycopersicon*, *Pinus*, *Hibiscus*, *Avena*, *Zea*, *Triticum*, *Panax*, *Citrus*, *Pelargonium*. Collected by various investigators and identified by Wollenweber and Carpenter.

*F. solani* (*sensu strict.*) is regarded as a saprophyte, but apparently it acts as a weak wound parasite under exceptionally favorable conditions.

2. *Fusarium coeruleum* (Lib.) Sacc. (1, p. 90).

Conidia normally triseptate (Pl. XIV, fig. 5), averaging 30 to 40 by 4.5 to 5.5 $\mu$  (limits of normal triseptate conidia: 23 to 47 by 4.25 to 6 $\mu$ ); seldom 4 and 5 septate (limits: triseptate, 23 by 4.25 $\mu$  minimum; 7-septate, 58 by 5.75 $\mu$  maximum). Conidial mass brownish white and yellow ochre to reddish ochre. Plectenchymatic stroma chiefly violet to indigo blue and bluish black; by infiltration with the latter color the conidial masses may become bluish green, as in other species of the section Martiella. *F. coeruleum* is the only species of the section having reddish ochre conidial masses. Chlamydospores as in other species of the section.

*Habitat*.—On tubers of *Solanum tuberosum*. Established as a cause of tuber rot in this country and in Europe by Wollenweber (20, p. 44). Determined by Dr. Wollenweber and the writer in material from the following localities: Ottawa, Canada; Houlton, Me.; Rhinebeck, N. Y.; Fredericksburg, Md.; Norfolk, Va.; Parkersburg, W. Va.; Donnybrook, N. Dak.; Idaho Falls, Idaho; Potlatch, Wash.; and several places in Oregon.

3. *Fusarium eumartii*, n. sp.

*F. eumartii* isolated from the Pennsylvania dry-rot agrees with Appel and Wollenweber's (1, p. 78-84) diagnosis of *F. martii* except in certain details of the conidia. The latter in the new species are higher septate and have a somewhat larger average size (Pl. XIV, fig. 4). Normally 4 to 6 septate, averaging 54 to 75 by 5.5 to 6.6 $\mu$  (limits: 50 to 80 by 5 to 7.2 $\mu$ ). Largest conidia 85 by 7.2 $\mu$  (7 and 8 septate). Percentages of variously septate conidia, average sizes and limits as found in a 10-day-old pionnotes on *Melilotus alba* and in a 15-day-old pionnotes on cotton are given in Table VII.

<sup>1</sup> For definition of these terms see Wollenweber, H. W. (20, p. 24).

TABLE VII.—Percentages of variously septate normal conidia, average sizes, and limits of size as found in a 10-day-old pionnotes on *Melilotus alba* and in a 15-day-old cotton pionnotes of *Fusarium eumartii*.

## 10-DAY-OLD PIONNOTES ON MELILOTUS ALBA

Septation.	Percentage of conidia.	Average size of conidia.	Limits.
		$\mu$	$\mu$
3.....	7	.....	.....
4.....	20	54.4 by 5.6.....	51 to 54.4 by 5.1 to 6.1.
5.....	50	63.7 by 5.8.....	59.5 to 69.7 by 5.4 to 6.1.
6.....	8	69.7 by 6.3.....	66.3 to 71.4 by 6.1 to 6.8.
7.....	15	71.6 by 6.5.....	68 to 76.5 by 5.9 to 6.8.

## 15-DAY-OLD PIONNOTES ON COTTON

3.....	5	.....	.....
4.....	17	.....	.....
5.....	58	62.9 by 6.1.....	56 to 76.5 by 5 to 6.8.
6.....	18	73.2 by 6.6.....	51 to 81.6 by 5.9 to 7.2.
7.....	2	79.9 by 6.6.....	74.8 to 85 by 6.3 to 6.8.
8.....	Rare.	85 by 6.8.....	.....

The formation of pigment in *F. eumartii* (Pl. A, fig. 6-8) and *F. radicola* is much the same as that in *F. solani*, only more gorgeous. The conidial color fluctuates between brownish white and bright brown; by infiltration of the greenish blue plectenchymatic pigment the conidial mass becomes gray, blue-green, to brown and a dark mixed color. The plectenchymatic stroma is weakly developed or lacking, and therefore the pionnotes lies naked on the substratum. The chlamydo-spores, 7 to 10 $\mu$  in diameter, agree with those in other species of this section.

*F. eumartii* causes a rot of potatoes in experiments, while *F. martii* is said to be a saprophyte (20, p. 30). This statement was confirmed with *F. martii* 186 collected in Germany. The new species agrees more closely with *Fusisporium solani* Martius (8) in the size of conidia than does *F. martii*.

*F. radicola* and *F. eumartii* are very closely related to *F. martii* with respect to average size and septation of normal conidia and occupy the same relative positions on either side of the last-mentioned species as a type. In average measurements the conidia of *F. radicola* are approximately 30 per cent shorter and 20 per cent narrower than those of *F. martii* (*sensu strict.*), while *F. eumartii* is larger in about the same proportion. *F. radicola* is typically triseptate, *F. martii* 3- to 4-septate, and the new species 5- to 6-septate. Similar constant varieties of certain other species are known—e. g., of *Fusarium solani*.

Habitat.—On decaying tubers of *Solanum tuberosum* from Pennsylvania and New York. Cause of potato dry-rot and wet-rot.

4. *Fusarium radicola* Wollenw. (21, p. 257-258).

The conidia of this species are normally triseptate, averaging 30 to 45 by 3.75 to 5 $\mu$ ; narrower than in *F. solani*, *sensu strict.* (Pl. XIV, fig. 3), and shorter and fewer septate than in *F. martii* and *F. eumartii* (Pl. XIV, fig. 4). The plectenchymatic mycelium, as in the two latter species, is olive colored on potato cylinders, shading to green and brown. Pionnotes on potato cylinders, cotton, and stems of *Melilotus alba* brownish white to blue and verdigris (Pl. A, fig. 6-8). Pigment formation the same as in *F. martii* and *F. eumartii*. Chlamydo-spores as in other species of the section.



Habitat.—On partly decayed tubers and roots of plants. Cause of potato dry-rot and jelly-end rot. Identified from the following: *Ipomoea batatas* (collected by Mr. L. L. Harter); *Musa sapientum* (collected by Mr. S. F. Ashby, Jamaica, Porto Rico); *Cucumis sativus* (collected by Mr. F. V. Rand, West Haven, Conn.); and (collected by Mr. F. C. Werkenthin, Austin, Tex.).

#### B. SECTION ELEGANS

[Species in this section are *F. oxysporum* Schlecht., *F. hyperoxysporum* Wollenw., *F. vasinfectum* Atk., *F. tracheiphilum* Sm., *F. niveum* Sm., *F. lycopersici* Sacc., *F. conglutinans* Wollenw., *F. redolens* Wollenw., *F. orthoceras* App. and Wollenw., *F. orthoceras*, var. *triseptatum* Wollenw., *F. batatas* Wollenw.]

1. *Fusarium oxysporum* Schlecht. (20, p. 28).

2. *Fusarium hyperoxysporum* Wollenw. (21, p. 268).

*F. oxysporum* (Pl. XIV, fig. 1) is not sharply differentiated morphologically from several species of this section—namely, *F. hyperoxysporum*, *F. vasinfectum*, *F. tracheiphilum*, *F. lycopersici*, and *F. niveum*. *F. hyperoxysporum* forms a perfect pionnotes in contrast to the reduced pionnotes in *F. oxysporum* (Pl. A, fig. 1-5). According to Harter and Field (4, p. 296), it is different biologically in that it causes a stem-rot of *Ipomoea batatas* and is not infectious on young plants of *Solanum tuberosum*, while *F. oxysporum* causes a wilt of the latter host but does not attack the former (21, p. 268). Both develop a lilac odor on starchy media. However, this character is of doubtful specific value since non-odor-forming strains of *F. oxysporum*, *F. hyperoxysporum*, and *F. vasinfectum* have been isolated, and some of the odor-forming strains temporarily lose this property in culture.

*F. tracheiphilum*, the cause of a wilt of species of *Vigna*, is without pionnotes and odor. *F. vasinfectum*, the cause of a wilt of cotton, develops a perfect pionnotes of an ochreous-salmon color; on potato cylinders in subdued light this color becomes slightly purple. Typically a strong lilac odor is present on starchy media. A non-odor-forming strain was designated *F. vasinfectum*, var. *inodoratum*, by Wollenweber (20, p. 29). *F. lycopersici*, the cause of a wilt of *Solanum lycopersicum*, differs from *F. oxysporum* in having conidia of a little larger average size and produces colorless sclerotial plectenchymatic masses in contrast to the bluish masses of this sort in *F. oxysporum*, etc. No odor is developed. *F. niveum*, to which the wilt of species of *Citrullus* is attributed, differs from *F. lycopersici* in forming blue sclerotial bodies on potato cylinders; from *F. oxysporum* in having larger conidia and no odor.

It is possible to determine the six above-mentioned species by morphological characters alone. Although a knowledge of the host of the particular species to be determined is not necessary, such information greatly facilitates the work. In spite of the fact that each of these forms seems to cause a wilt on one particular host, it should be pointed out that too much dependence on the value of the host in descriptions of species has led to the present confusion in the nomenclature of the form genus *Fusarium*.

A species of *Fusarium* causing a field soft-rot of Irish potatoes in Mississippi (Pl. XV, fig. 1, 2) was morphologically identical with *F. oxysporum* (Pl. XIV, fig. 1), but developed a perfect pionnotes on potato cylinders (Pl. A, fig. 4); thus, it must be identical with *F. hyperoxysporum*, the cause of stem-rot of the sweet potato. Inoculation with *F. hyperoxysporum* isolated by Harter and Field from the latter host resulted in complete destruction of the tubers (see No. 3399 and reisolation of same, No. 3489, p. 192), indicating the truth of the hypothesis.

Further cross-inoculation work carefully controlled by morphological studies should demonstrate whether all of the above-mentioned species of this section are biologically distinct; whether, for example, *F. hyperoxysporum* differs sufficiently from *F. oxysporum*, on the one hand, and *F. vasinfectum*, on the other, to be entitled to the rank of species.

## C. SECTION DISCOLOR

(Species in this section are *F. discolor* App. and Wollenw.; *F. discolor*, var. *sulphureum* (Schlecht.) App. and Wollenw.; *F. culmorum* (W. G. Sm.) Sacc. (syn., *F. rubiginosum* App. and Wollenw.); *F. trichothecioides* Wollenw.; and *F. incarnatum* (Rob.) Sacc.)

1. *Fusarium discolor*, var. *sulphureum* (Schlecht.) App. and Wollenw. (1, p. 115-118).

*F. discolor*, var. *sulphureum*, is morphologically the same as *F. discolor* App. and Wollenw. (1, p. 114). Normal conidia (Pl. XIV, fig. 6) 3- to 5-septate, 23 to 39 by 4.5 to 5.5 $\mu$  (limits: 16 to 48 by 3.5 to 6 $\mu$ ); exceptionally 1- and 2-septate. True chlamydospores are rare. Conidial masses ochreous to ochreous-orange. Differs from *F. discolor* in the color of the plectenchymatic mycelium, which never becomes carmine-red (Pl. B.), but changes from ochreous to yellow (egg-yellow to sulphur-yellow, which color permeates the aerial mycelium and conidial masses).

Habitat.—In hollows of potato tubers. Established by Dr. Wollenweber as the cause of a tuber-rot in Germany. It was isolated from decaying tubers from Newell, S. Dak., and identified by Dr. Wollenweber. The writer also identified it in similar material from Cresbard, S. Dak., and in tubers from the North Dakota Agricultural College (collected by Mr. D. G. Milbrath).

2. *Fusarium trichothecioides* Wollenw. (5, p. 146-152).

*F. trichothecioides*, in contrast to the other species of the section *Discolor*, forms two sorts of conidia: (1) The comma type, formed as a slightly curved comma ellipsoidally rounded on both sides; and (2) the normal macroconidia, typical of the section. The plectenchymatic mycelium and conidial masses are rosy white, in contrast to the carmine<sup>1</sup> mycelium in *F. discolor* (Pl. B, fig. 1-3) and the ochreous-yellow mycelium in *F. discolor*, var. *sulphureum* (Pl. B, fig. 4-6). The conidial masses in both the last-named species are ochreous orange.

Habitat.—Dry-rotting tubers of *Solanum tuberosum*, causing decay, especially under storage conditions. Geographic distribution: Spokane, Wash.; St. Paul, Minn.; Dayton, Iowa; Alliance, Nebr.; Spearfish, S. Dak. (Jamieson and Wollenweber). The following localities are added to the above: Jerome and Idaho Falls, Idaho; Newell, S. Dak.; and Sioux City, Iowa.

## SUMMARY

(1) A new stem-end and wound-invading dry-rot of the Irish potato annually causing serious damage in Pennsylvania is caused by a species of *Fusarium* for which the name "*Fusarium eumartii*" is proposed.

(2) Another widely prevalent dry-rot similar to the above is caused by *F. radicicola* Wollenw.

(3) *F. radicicola* and *F. oxysporum* are most commonly associated with the so-called "jelly-end" rot, annually a serious trouble in the tule lands of California. The former seems to be the cause in most cases, but the fundamental relationship of *F. oxysporum* to this and other tuber-rots should not be overlooked.

(4) Experimental inoculations show that *F. oxysporum* and *F. hyperoxysporum*, species of the section *Elegans*, which has been reported as containing purely vascular parasites, are capable of entirely destroying potato tubers.

(5) *F. oxysporum* is the cause of certain types of tuber-rot.

<sup>1</sup> Jamieson and Wollenweber (5) give "purple" mycelium through error.

(6) *F. radicola* caused no rot at 12° C. A constant storage temperature below 50° F. would prevent the action of *F. radicola*, *F. eumartii*, and *F. oxysporum*.

(7) The following species of *Fusarium* are added to those known to cause tuber-rot through wound infection: *F. radicola* Wollenw.; *F. eumartii*, n. sp.; *F. oxysporum* Schlecht.; and *F. hyperoxysporum* Wollenw.

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## PLATE A

### *Fusarium* spp. on vegetable media:

Fig. 1-3 and 5.—*Fusarium oxysporum* Schlecht. 3045. 1, Twenty-one-day-old culture on potato cylinder showing typical bluish green sclerotial masses, no pionnotes. 2, Eighteen-day-old culture on stem of *Melilotus alba* with pionnotes. 3, Eighteen-day-old rice culture with typical coloration of the section Elegans. 5, Thirty-day-old cotton-stem culture with sporodochia.

Fig. 4.—*F. hyperoxysporum* Wollenw. 3343. Thirty-one-day-old culture on potato cylinder with development of pionnotes. Cultures on the three other media are as illustrated for *F. oxysporum* (fig. 1-3, 5).

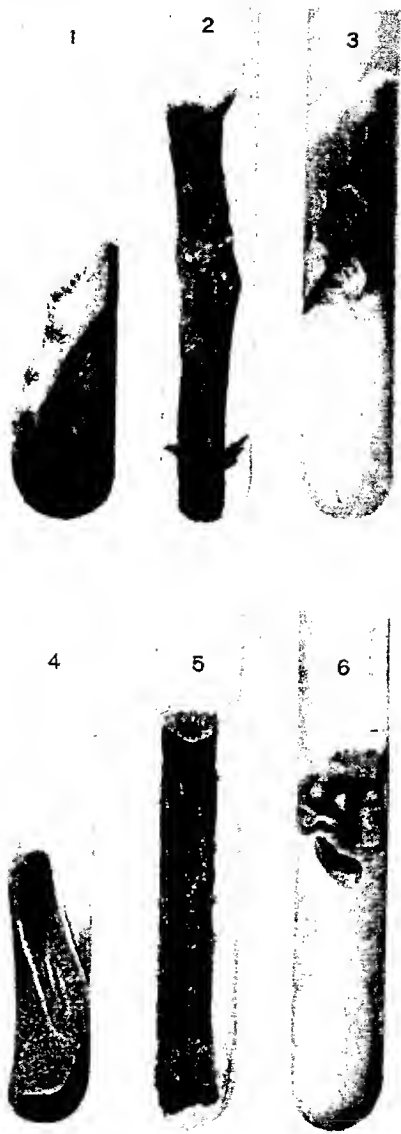
Fig. 6-8.—*F. radicicola* Wollenw.; illustrates equally well *F. martii* and *F. cumarii*. 6, Potato cylinder 34 days old with pionnotes brown to verdigris. 7, Seventeen-day-old culture on stem of *Melilotus alba* with pionnotes and immature sporodochia. 8, Rice 28 days old, with pionnotes on upper surface. Coloration of the section Martiella.











## PLATE B

### *Fusarium* spp. on vegetable media:

Fig. 1-3.—*Fusarium discolor* Appel and Wollenw. 153, showing typical color reactions of this type species of the section *Discolor*. This section includes *F. trichothecoides* and *F. discolor*, var. *sulphureum*, both of which differ from the type in color reactions. 1, Potato cylinder 11 days old, showing carmine red pigmentation of the plectenchymatic mycelium. 2, Culture on cotton stem 35 days old, showing sporodochia and pionnotes drying out. 3, Rice culture 11 days old.

Fig. 4-6.—*F. discolor*, var. *sulphureum* (Schlecht.) Appel and Wollenw. 154. 4, Ocherous-orange pionnotes on 11-day-old potato cylinder. 5, Sporodochia on 39-day-old cotton-stem culture. 6, Rice culture 11 days old.

#### PLATE XIV

Fig. 1.—*Fusarium oxysporum* Schlecht: A, Normal conidia. B, Swollen conidia, the first one exceptionally long and high septate. C, Conidio-chlamydospores. D, Young intercalary and terminal chlamydospores.  $\times 1,000$ .

Fig. 2.—*F. radicicola* Wollenw. Normal conidia.  $\times 1,000$ .

Fig. 3.—*F. solani* (Mart.) Sacc. Type species of the section Martiella. Normal conidia.  $\times 1,000$ .

Fig. 4.—*F. eumartii*, n. sp. Normal conidia.  $\times 1,000$ .

Fig. 5.—*F. coeruleum* (Lib.) Sacc. Normal conidia.  $\times 1,000$ .

Fig. 6.—*F. discolor*, var. *sulphureum* (Schlecht.) App. and Wollenw. Normal conidia.  $\times 1,000$ .

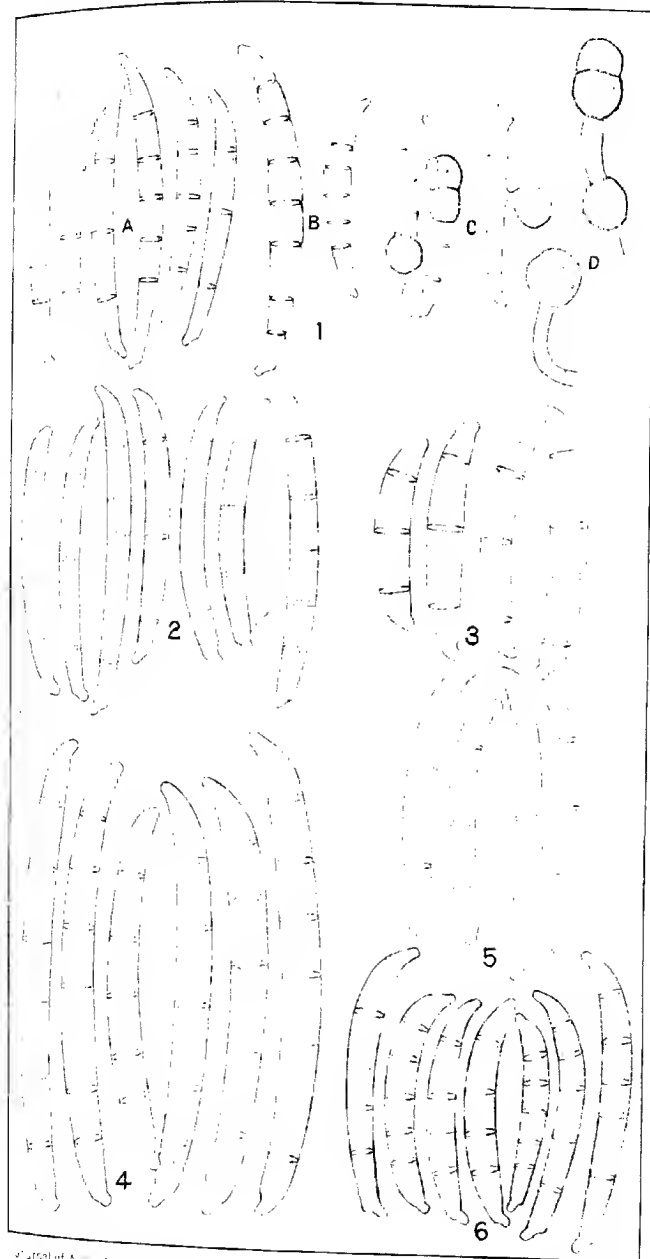




PLATE XV

Fig. 1, 2.—Potato tuber showing a soft-rot caused by *Fusarium hyperoxysporum* Wollenw. Field material from Mississippi.

Fig. 3.—Potato tuber showing the type of rot produced by *F. oxysporum* in the experiments. Idaho Rural variety of potato inoculated with *F. oxysporum* 2999.

Fig. 4, 5.—Potato tuber showing a dry-rot caused by *F. radicicola*, from high ground, Sonora, Cal.

PLATE XVI

Two "jelly end" tubers from Moorland, Cal., showing external views and longitudinal sections.





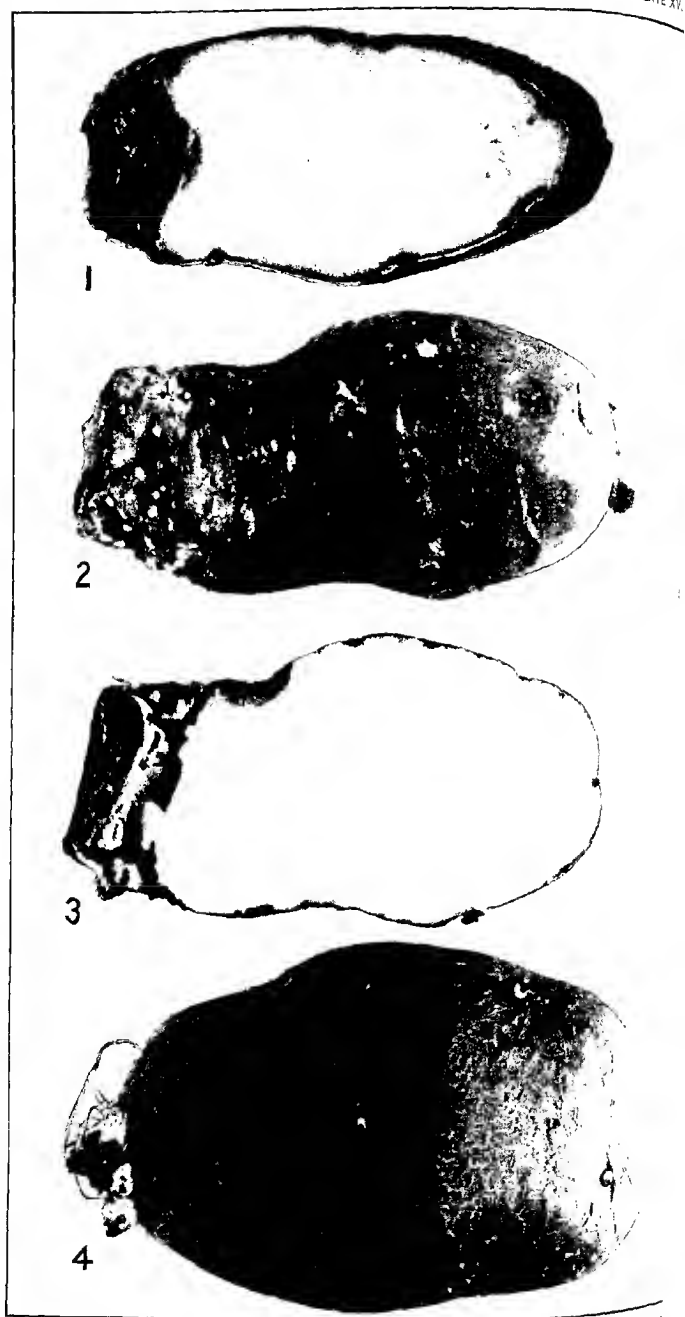


PLATE XVII

"Jelly-end" rot produced by inoculation with *Fusarium radicicola* Wollenw.:

Fig. 1.—Control potato tuber.

Fig. 2, 3, 4.—Potato tuber inoculated with *F. radicicola* 2890; isolated from material similar to that shown in Plate XVI.

## PLATE XVIII

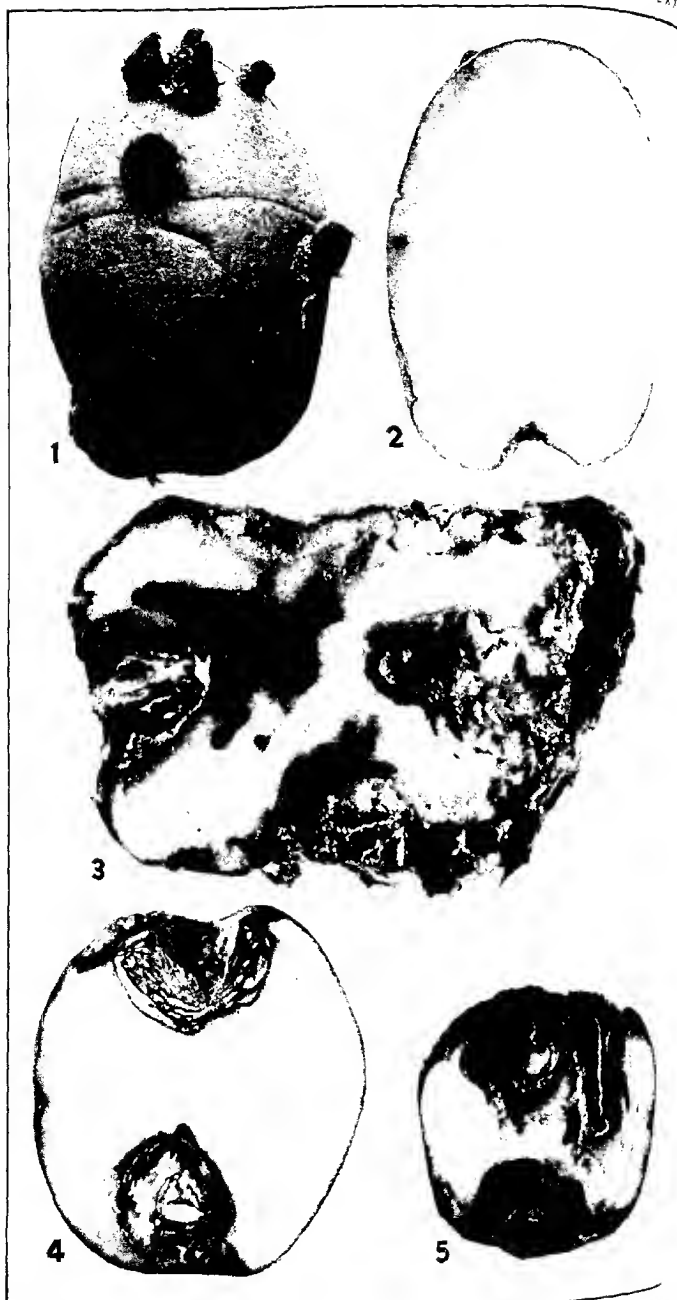
Tuber-rot from Pennsylvania caused by *Fusarium eumartii*, n. sp.:

Fig. 1, 2.—External and sectional view of the same potato tuber. The spots in the center of figure 2 are not pertinent.

Fig. 3, 4.—Sectional views of other potato tubers.

Fig. 5.—A cross section of a potato tuber showing how the fungus frequently follows the tissue adjacent to the bundle ring.





#### PLATE XIX

Tuber-rot produced in the laboratory with *Fusarium eumartii*, n. sp., and control potato tuber:

Fig. 1, 2.—Control.

Fig. 3.—Potato tubers showing a soft-rot, as a result of rapid development. Incubation period 19 days at room temperature. People's variety.

Fig. 4, 5.—Potato tubers selected to illustrate the type of rot in slower development. Jersey Peachblow variety.



## INFECTION EXPERIMENTS WITH TIMOTHY RUST

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### INTRODUCTION

There is some diversity of opinion as to whether or not timothy rust should be regarded as a distinct species. Eriksson and Henning (2, p. 140-142)<sup>1</sup> in 1894 designated it "*Puccinia phleipratensis* Eriks. u. Henn." Johnson (4) decided that timothy rust in this country was the same as that in Sweden and favors giving the fungus specific rank. Kern (5, 6), on the other hand, thinks it should be considered as a physiological species, or, at most, a variety or subspecies.

It is therefore of interest to know the infection capabilities of the rust. Eriksson and Henning (3, p. 136-141), reported the successful infection of rye (*Secale cereale*) and oats (*Avena sativa*), but none of wheat (*Triticum vulgare*) or barley (*Hordeum vulgare*). Johnson (4, p. 9) obtained results confirming those of Eriksson and Henning. Johnson also succeeded in successfully infecting a number of grasses. He found that the rust would not transfer directly to barley, but if transferred first to oats and then to barley infection resulted. In the same way *Dactylis glomerata* acted as a bridging form between timothy and wheat. Mercer (7) was unable to obtain successful infection on wheat, rye, and various grasses as a result of inoculations made with timothy-rust urediniospores.

The inoculations made by the writers were all on seedlings. The leaves were first thoroughly moistened either with an atomizer or by rubbing water on with the fingers. The spores were applied with a flat inoculating needle. The plants were then placed in shallow pans of water and kept covered with bell jars for 48 hours. The grass seeds were obtained from the Minnesota Seed Laboratory. The following varieties of cereals were used: Oats, Improved Ligowa, Minn. No. 281; barley, Manchuria, Minn. No. 105; wheat, Bluestem, Minn. No. 169; rye, Swedish, Minn. No. 2.

### RESULTS OF INOCULATIONS

The writers made a number of inoculations with timothy-rust urediniospores, the results of which are given in Table I.

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<sup>1</sup> Reference is made by number to "Literature cited," p. 216.



TABLE I.—Results of inoculations with timothy-rust urediniospores on cereals and grasses

Date of inoculation.	Source of urediniospores.	Plant inoculated.	Number of leaves inoculated.	Number of leaves infected.
Dec. 18, 1914.	<i>Phleum pratense</i> .....	<i>Triticum vulgare</i> .....	37	0
Dec. 24, 1914.	do.....	do.....	20	0
Dec. 29, 1914.	do.....	do.....	41	0
Jan. 16, 1915.	do.....	do.....	53	0
Dec. 18, 1914.	do.....	<i>Avena sativa</i> .....	25	0
Dec. 24, 1914.	do.....	do.....	20	2
Jan. 9, 1915.	do.....	do.....	23	0
Jan. 17, 1915.	do.....	do.....	107	14
Feb. 19, 1915.	do.....	do.....	40	1
Dec. 18, 1914.	do.....	<i>Hordeum vulgare</i> .....	31	0
Dec. 24, 1914.	do.....	do.....	31	0
Dec. 29, 1914.	do.....	do.....	31	2
Jan. 26, 1915.	do.....	do.....	48	12
Feb. 1, 1915.	do.....	do.....	23	1
Dec. 18, 1914.	do.....	<i>Secale cereale</i> .....	11	0
Dec. 24, 1914.	do.....	do.....	14	0
Dec. 29, 1914.	do.....	do.....	38	0
Feb. 1, 1915.	do.....	do.....	39	1
Feb. 19, 1915.	do.....	do.....	41	6
Apr. 3, 1915.	do.....	<i>Avena fatua</i> .....	7	3
Apr. 11, 1915.	do.....	do.....	15	2
Apr. 3, 1915.	do.....	<i>Avena elatior</i> .....	20	3
May 29, 1915.	do.....	<i>Bromus tectorum</i> .....	23	3
Jan. 12, 1915.	do.....	<i>Dactylis glomerata</i> .....	55	37
Jan. 14, 1915.	do.....	<i>Elymus virginicus</i> .....	40	1
Apr. 11, 1915.	do.....	<i>Lolium italicum</i> .....	31	0
May 29, 1915.	do.....	do.....	31	0
Do.....	do.....	<i>Lolium perenne</i> .....	15	3
Do.....	do.....	do.....	40	4
Mar. 3, 1915.	<i>Hordeum vulgare</i> .....	<i>Phleum pratense</i> .....	48	0
Mar. 14, 1915.	do.....	do.....	40	0
Mar. 7, 1915.	<i>Avena sativa</i> .....	do.....	71	0
Apr. 11, 1915.	<i>Avena fatua</i> .....	do.....	34	0
Apr. 18, 1915.	do.....	do.....	18	0
May 2, 1915.	<i>Phalaris canariensis</i> .....	do.....	25	0
Mar. 7, 1915.	<i>Dactylis glomerata</i> .....	do.....	40	0
Mar. 14, 1915.	do.....	do.....	50	0

## SUMMARY.

Source of inoculating material.	Plant inoculated.	Result of inoculation. <sup>a</sup>	Source of inoculating material.	Plant inoculated.	Result of inoculation. <sup>d</sup>
<i>Phleum pratense</i> ...	<i>Triticum vulgare</i> ...	0 150	<i>Phleum pratense</i> ...	<i>Lolium italicum</i> ...	1 31
Do.....	<i>Avena sativa</i> .....	37 195	Do.....	<i>Lolium perenne</i> ...	1 31
Do.....	<i>Hordeum vulgare</i> ...	24 154	Do.....	<i>Bromus tectorum</i> ...	1 23
Do.....	<i>Secale cereale</i> .....	8 143	<i>Hordeum vulgare</i> ...	<i>Phleum pratense</i> ...	0 48
Do.....	<i>Avena fatua</i> .....	6 17	<i>Avena sativa</i> .....	do.....	0 71
Do.....	<i>Avena elatior</i> .....	3 20	<i>Avena fatua</i> .....	do.....	0 34
Do.....	<i>Dactylis glomerata</i> ...	37 55	<i>Phalaris canariensis</i> ...	do.....	0 25
Do.....	<i>Elymus virginicus</i> ...	1 40	<i>Dactylis glomerata</i> ...	do.....	0 40

<sup>a</sup> *Puccinia graminis*, originally from *Hordeum jubatum*; on barley 8 urediniospore "generations."<sup>b</sup> *Puccinia graminis*, originally from *Dactylis glomerata*; on oats 9 urediniospore generations.<sup>c</sup> *Dactylis glomerata* rust after 15 generations on oats and one generation on *Phalaris canariensis*.<sup>d</sup> The denominator gives the total number of leaves inoculated, the numerator the number which developed pustules.

It will thus be seen that the rust from timothy transfers directly to three of the common cereals. Neither Eriksson and Henning (3) nor Johnson (4), as previously mentioned, were able to obtain successful infection on barley as a result of direct transfer from timothy. However, the writers were able to infect some plants in four of the five series of inoculations. The percentage of infections on barley is nearly as great as that on oats and is greater than that on rye. The rust transferred very readily to *Dactylis glomerata* and fairly well to both *Avena elatior* (*Arrhenatherum elatius*) and *Avena fatua*. It also transferred to *Lolium perenne*, *Lolium italicum*, and *Bromus tectorum*. One extremely small pustule developed on *Elymus virginicus*.

The vigor of infection varied greatly on different hosts. In addition to the inoculations indicated in Table I, many inoculations were made on timothy. These nearly always resulted in a 100 per cent infection. The incubation period on timothy was 7 to 8 days, while on barley it was 10 to 12 days. It was clearly evident that barley was an uncongenial host; fairly large dead areas were frequently formed without subsequent development of pustules, and all pustules, when they did develop, were extremely small. Most of the pustules were less than 1 mm. in diameter, being mere dots in some cases. However, others were somewhat larger, some attaining a diameter of over 1 mm. On oats the pustules were larger, the rust developing in a fairly normal manner. The pustules on rye were fairly small, but there was not such a distinct tendency to produce flecks as there was on barley. The infection on *Avena elatior*, *Avena fatua*, *Lolium perenne*, and *Lolium italicum* was moderate, while that on *Dactylis glomerata* was very severe, nearly as severe as that on timothy. On *Bromus tectorum* the pustules were extremely small.

Although the rust transferred fairly readily from timothy to both barley and oats, no infection was obtained on timothy as a result of inoculations with *Puccinia graminis hordei* and *Puccinia graminis avenae*. Less than 100 inoculations were made with *Puccinia graminis hordei*; in no case, however, was there any indication of successful infection. The transfer is entirely possible; more inoculations will therefore be made. Timothy was inoculated directly with *Puccinia graminis avenae*, but no infection resulted from any of 86 trials. No better results were obtained by transferring first to *Avena fatua*, *Phalaris canariensis*, or *Dactylis glomerata*. None of these forms, therefore, acted as a bridging form between oats and timothy. It is possible that such bridging forms may exist, although the possibility has not yet been demonstrated. Carleton (1, p. 62) reported successful infection of *Puccinia graminis avenae* on *Phleum asperum*. It is possible that this form might act as a bridging species, but the writers have not yet had opportunity to determine this.

## EXPERIMENTS WITH BRIDGING HOSTS

Johnson (4, p. 10) found that by using *Avena sativa* as a bridging host the timothy rust could be transferred to *Hordeum vulgare*; by using *Festuca elatior* it could be transferred to *Hordeum vulgare* and to *Triticum vulgare*; by using *Dactylis glomerata* it could be transferred to *Triticum vulgare*. Since the writers were able to infect barley directly, but not wheat, without the bridging hosts, an attempt was made to determine whether or not, with the strain of rust employed, it would be possible to make transfers to wheat after using *Dactylis glomerata* as a bridging form and whether or not the rust would transfer to barley more readily under the same conditions. Transfers were made from timothy to *Dactylis glomerata*, and heavy infection was obtained. Two series of inoculations were then made with spores from *Dactylis glomerata* to wheat, oats, barley, rye, and timothy. The results were as follows: Wheat,  $\frac{1}{17}$ ; oats,  $\frac{2}{34}$ ; barley,  $\frac{2}{34}$ ; rye,  $\frac{2}{34}$ ; timothy,  $\frac{1}{17}$ . When oats was used as a bridging host, approximately the same percentage of infections resulted as when the rust was transferred directly from timothy. The writers were, therefore, unable to increase the infection capabilities of the rust by means of first transferring to *Dactylis glomerata* or oats. Neither was the vigor of infection appreciably greater on barley and oats after using bridging species. It is possible that by confining the rust for a long series of generations on a bridging host definite results might be obtained. Such experiments are now under way.

The results cited show that different results may be obtained with different strains of rust. That Johnson (4) and Eriksson and Henning (3) worked with different strains seems entirely probable, in view of the fact that neither was able to transfer the rust directly to barley, while the writers experienced no particular difficulty in making such transfer. The possibility of conflicting results may be clearly shown by results which the writers have recently obtained. Timothy rust and stem rust of oats (*Puccinia graminis avenae*) transferred very readily to *Dactylis glomerata*. But the rusts by no means acquired the same capabilities as a result of growing on *Dactylis glomerata*, at least not in a few generations. When the timothy rust on *Dactylis glomerata* was transferred to oats less than 10 per cent of the inoculated leaves became infected; when the rust was transferred to barley very small pustules were produced on about 16 per cent of the inoculated leaves; when it was transferred to rye, small pustules were produced on about 6 per cent of the inoculated leaves; when it was transferred to timothy 95 per cent of the leaves became infected. When, on the other hand, stem-rust of oats (*P. graminis avenae*) on *Dactylis glomerata* was transferred to oats, 100 per cent of the inoculated leaves became very severely affected; inoculations on barley resulted in 7 per cent of infection; inoculations on rye resulted in no infection (in other experiments the writers have been able to infect

rye with *P. graminis avenae*); no infection resulted from inoculations on timothy. The writers also have two strains of *Puccinia graminis*, both of which have been confined to the same variety of barley for nine months. Both attack barley and a number of wild grasses very readily; neither has ever infected oats; one attacks wheat with extreme vigor and infects rye only with difficulty, while the other is almost entirely unable to infect wheat but attacks rye with great vigor.

It seems fairly clear that, as Johnson (4, p. 10) has previously pointed out, timothy rust and *Puccinia graminis avenae* are quite similar. Both rusts transferred to *Dactylis glomerata*, *Avena fatua*, *Avena elatior*, barley, rye, *Lolium perenne*, *Lolium italicum*, *Bromus tectorum*, and *Elymus* spp.; the oats rust to *Elymus robustus* and *Elymus canadensis*; and the timothy rust to *Elymus virginicus*. With the exception of *Avena fatua*, they transferred with somewhat the same degree of readiness.

#### MORPHOLOGY OF THE SPORES

Morphologically, however, the two rusts are somewhat different, the spores of *Puccinia graminis avenae* being larger. Spores of *Puccinia graminis avenae*, originally from *Dactylis glomerata* and then confined to oats for 14 successive generations, ranged from 19 to 35 $\mu$  in length and from 16 to 24 $\mu$  in width, the modes falling at about 30 and 19 $\mu$ . The spores of timothy rust on timothy ranged from 17 to 31 $\mu$  in length and from 14.5 to 23 $\mu$  in width, the modes falling at about 26 and 18 $\mu$ . After one generation on *Dactylis glomerata*, the timothy-rust spores ranged from 17 to 32 $\mu$  in length, and from 13.5 to 23.2 $\mu$  in width, while the modes fell at about 25.5 and 19.5 $\mu$ . At least 100 spores from different pustules were measured. Measurements were also made of spores produced after the rust had been one generation on other hosts, including oats, rye, barley, *Lolium perenne*, and *Avena fatua*; but no distinct and consistent differences were apparent, with the exception of the spores produced on barley. These were smaller than those produced on any other host, ranging from 18.5 to 28.3 $\mu$  in length and from 13 to 20 $\mu$  in width. The modes were at about 23 and 17 $\mu$ . Whether or not greater variations would occur if the rust were confined to the different hosts for longer periods of time is not yet known. Experiments have been begun to determine the effect of different hosts on the morphology of the spores.

#### SUMMARY

- (1) Timothy rust was transferred successfully directly from timothy to *Avena sativa*, *Hordeum vulgare*, *Secale cereale*, *Avena fatua*, *Avena elatior*, *Dactylis glomerata*, *Elymus virginicus*, *Lolium italicum*, *Lolium perenne*, and *Bromus tectorum*.
- (2) Attempts to increase the infection capabilities of the rust by the use of bridging hosts for short periods of time were unsuccessful.

(3) The infection capabilities of timothy rust are quite similar to those of *Puccinia graminis avenae*.

(4) Attempts to infect timothy with *Puccinia graminis avenae* and *Puccinia graminis hordei* were unsuccessful.

(5) The morphology of the spores of timothy rust on different hosts varies slightly; spores produced on barley were considerably smaller than those produced on more congenial hosts.

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